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REVIEW

What can whiskers tell us about mammalian evolution, behaviour, and ecology?

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ABSTRACT

1. Most mammals have whiskers; however, nearly everything we know about whiskers derives from just a handful of species, including laboratory rats *Rattus norvegicus* and mice *Mus musculus*, as well as some species of pinniped and marsupial.
2. We explore the extent to which the knowledge of the whisker system from a handful of species applies to mammals generally. This will help us understand whisker evolution and function, in order to gain more insights into mammalian behaviour and ecology.
3. This review is structured around Tinbergen's four questions, since this method is an established, comprehensive, and logical approach to studying behaviour. We ask: how do whiskers work, develop, and evolve? And what are they for?
4. While whiskers are all slender, curved, tapered, keratinised hairs that transmit vibrotactile information, we show that there are marked differences between species with respect to whisker arrangement, numbers, length, musculature, development, and growth cycles.
5. The conservation of form and a common muscle architecture in mammals suggests that early mammals had whiskers. Whiskers may have been functional even in therapsids.
6. However, certain extant mammalian species are equipped with especially long and sensitive whiskers, in particular nocturnal, arboreal species, and aquatic species, which live in complex environments and hunt moving prey.
7. Knowledge of whiskers and whisker use can guide us in developing conservation protocols and designing enriched enclosures for captive mammals.
8. We suggest that further comparative studies, embracing a wider variety of mammalian species, are required before one can make large-scale predictions relating to evolution and function of whiskers. More research is needed to develop robust techniques to enhance the welfare and conservation of mammals.

INTRODUCTION

Nearly all mammals have whiskers – sensory tactile hairs, also known as vibrissae (Fig. 1). They are only truly absent in a handful of species, including humans. Niko Tinbergen proposed that, by posing four questions, it is possible to explain a behaviour truly (Tinbergen 1963). In our case, the questions are as follows: how do whiskers work, develop, and evolve? And what are they for? We believe that Tinbergen's approach offers an established, comprehensive, and interlinked perspective for understanding

Fig. 1. Diversity of whisker arrangements and shapes. Top row (from left): brown rat *Rattus norvegicus* (photograph: Maria Panagiotidi, University of Salford, Salford, UK) and example whisker, harbour seal *Phoca vitulina* (photograph: Alyx Milne, Rhyl SeaQuarium, Rhyl, UK) and example whisker. Middle row (from left): grey short-tailed opossum *Monodelphis domestica* (photograph: Tony Prescott, University of Sheffield, Sheffield, UK), northern short-tailed shrew *Blarina brevicauda* (photograph: Gilles Gonthier, Flickr), ring-tailed lemur *Lemur catta* (photograph: Mathias Appel, Wikimedia), Pacific walrus *Odobenus rosmarus* (photograph: Alyx Milne, Dolfinarium Harderwijk, Harderwijk, the Netherlands). Bottom row (from left): Amazon river dolphin *Inia geoffrensis* (photograph: Luciana Christante, Flickr), Malayan flying fox *Pteropus vampyrus* (photograph: Lance Cheung, U.S. Department of Agriculture, Washington D.C., USA), Iberian wolf *Canis lupus* (photograph: Shaun Wilson, Blackpool Zoo, Blackpool, UK), horse *Equus ferus* (photograph: Brent M., Flickr).

animal behaviour. Therefore, in this review, we adopt Tinbergen's approach to present a 'state-of-the-art' snapshot of what is known about how different species use their whiskers, drawing information from studies of whisker anatomy, development, evolution, and function. We also consider the applications of whisker research for mammalian behaviour, welfare, and conservation.

Early 20th Century natural history studies on whisker biology were focused on documenting whisker presence and position in different species (Beddard 1902, Pocock 1914). Researchers found prominent whiskers on the upper lip, cheeks, lower lip, brow, cheeks, and forelegs of mammals (Vincent 1913, Pocock 1914). However, it is the long, mobile cheek whiskers (mystacial macrovibrissae), which have excited the most interest and which are the focus of this review. Comparative anatomy studies of whisker arrangements, follicles and their associated neural architecture and behaviour prevailed into the 1960s and 1970s (Klingener & Arbor 1964, Cave 1969, Welker 1973, Woolsey et al. 1975, Ahl 1986). However, since the 1970s, research has been centred on the whiskers of laboratory rats *Rattus norvegicus* and mice *Mus musculus*, especially by neuroscientists investigating sensory processing and motor control (Prescott et al. 2011, Evans et al. 2019). Some other species have also fallen under the scrutiny of researchers, including some species of pinnipeds, marsupials, and sirenians (Reep et al. 2001, Mitchinson et al. 2011, Grant et al. 2013a, Dehnhardt & Hanke 2018, Milne et al. 2020). Perhaps these species have been focused on due to the prominence of their whiskers; they are also held in captive collections, such as zoo and laboratories, so are more accessible to some researchers too. One consequence of such a narrow focus, on only a few species, is that comparative questions relating to evolution and function are difficult to address. Furthermore, very little can be known about the sensory ecology and behaviour of rare or elusive species.

Comparative whisker research can involve practical challenges. For example, anatomical studies are complex and time-consuming (Marshall et al. 2006, Grant et al. 2013a). Behavioural research relating to whiskers is often restricted by requirements for accessing and training an animal,

therefore limiting it to species within captive collections. Furthermore, these behavioural studies usually require species-specific set-ups and training protocols (Dehnhardt & Dücker 1996, Grant et al. 2013b, Arkley et al. 2014). However, recent developments in cameras and scanning technology, image processing techniques, and phylogenetic analysis techniques offer new possibilities for comparative whisker studies incorporating more species. Hence, a review is timely.

In this review, we endeavour to identify and answer key questions in relation to whisker evolution, form, and function. We additionally consider the implications of research on whiskers for animal behaviour, welfare, and conservation. We find that, while comparative whisker research has increased in recent years, more information is needed to address specific questions about whisker evolution and function.

METHODS

The structure of this narrative review is based around Tinbergen's four questions, as an established perspective for comprehensively describing animal behaviour. We also include a section on whisker applications to showcase the use of this research in mammalian management. In this way, the five review sections (four questions and one application section) are treated separately, with slightly different literature searches conducted in the order documented below. The 'how do whiskers work?' section has a deliberate bias away from laboratory rats and mice. Comprehensive reviews for those can be found in Diamond et al. (2008), Campagner et al. (2018), and Evans et al. (2019). Instead, we offer a broad survey of literature, embracing a much wider range of species, with the aim of providing information sufficient for the reader to follow the subsequent sections.

For the other four review sections, all literature searches were conducted in PubMed and Google Scholar from May to June 2020. All types of articles were considered for inclusion. Articles that were not available or were not in English were not included. From the articles retrieved in the first round of searches, additional references were identified by a manual search among the cited references (in agreement with the protocol outlined by Green et al. 2006). All searches included the search terms whiskers or vibrissa*. The 'how do whiskers develop?' search additionally incorporated the search terms development or growth; rat, cat, wallaby, and guinea pig were added following reading of the first round of references. The 'how did whiskers evolve?' search included search terms evolution, sensing, hair, and mammal, with synapsid and therapsid later added. The 'what are whiskers for?' search included articles from previous searches, with the addition of the search terms seal, sea lion, enrichment, locomotion, and foraging. The 'applications of comparative whisker studies' section includes articles from previous searches, with the addition of the search terms isotope, conservation, and identification. Each article was read to ensure its fit to this review. With narrative reviews, it is not necessary to include every article on a topic. For the applications section, for example, articles were only included when they presented the method for the first time; the results that arose from using whiskers in applied conservation research were considered to be outside the scope of this review.

HOW DO WHISKERS WORK?

Whiskers are slender rod-like structures that, like pelage hair, are made of keratin. They have a layered cross-section, involving a cuticle, medulla, and cortex (Voges et al. 2012, Belli et al. 2017). In general, whiskers are longer and thicker than pelage hair and their follicles are much larger and highly innervated. Most whiskers have near-circular cross-sections (whereas pelage hair tends to be oval), apart from seal (Phocidae) and sea lion (Otariidae) whiskers, which are oval, perhaps for reducing form drag in the water (Ginter et al. 2009, 2012). Whiskers are relatively smooth along their surface, although those of phocids have undulating or beaded profiles, also thought to be an adaptation to water (Ginter et al. 2009, Hanke et al. 2010, Ginter et al. 2012) Whiskers tend to be tapered; i.e., the cross-section at the tip is smaller than at the base, which means that they are more flexible towards the tip (Belli et al. 2017). This increasing flexibility is partly counteracted by a corresponding increase in the elastic (Young's) modulus towards the whisker tip (Quist et al. 2011). Nevertheless, the effect of tapering is dominant and increased flexibility at the tip is thought to enable better sensing, especially when distinguishing textures (Williams & Kramer 2010, Hires et al. 2013). Whiskers are also intrinsically curved, and a linear variation of curvature from base to tip is a good description for many species (Dougill et al. 2020, Starostin et al. 2020), which also lends support for whiskers having a linear growth rate (Ibrahim & Wright 1975, Hirons et al. 2001, Greaves et al. 2004).

On the whole, mystacial whiskers are arranged in ordered rows and columns (Woolsey et al. 1975; Fig. 2a). The grid system is particularly prominent in nocturnal, arboreal, and aquatic mammals, whereas diurnal visual mammals, such as horses, deer, and apes, tend to have fewer and less-organised whiskers (Muchlinski et al. 2013, Grant et al. 2017, Muchlinski et al. 2020, Fig. 1). The observed reduction in whisker organisation, length, and number in those latter species is probably linked to a corresponding reliance on their other senses, such as vision, hearing, or olfaction.

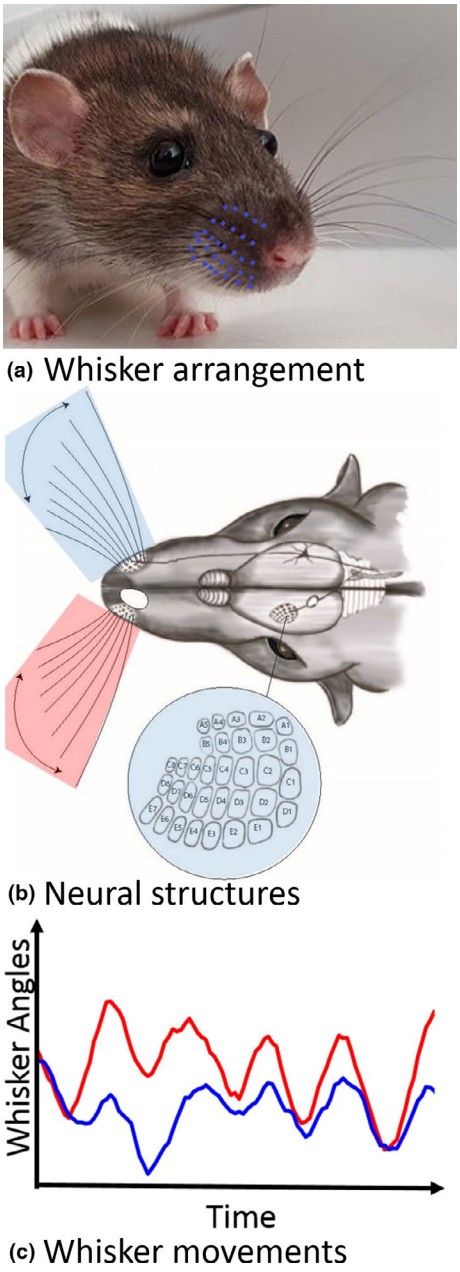

Fig. 2. Brown rat *Rattus norvegicus* whisker arrangement (a), topographic brain structures (b), and example movements shown as left and right angular whisker traces (c). Photograph: Maria Panagiotidi, University of Salford, Salford, UK.

Whiskers bend when they contact a surface. That bending is sensed by mechanoreceptors within the follicles that translate forces and moments into neural signals (Diamond et al. 2008, Campagner et al. 2018, Evans et al. 2019). Aquatic mammals, such as pinnipeds, have ten times more nerve endings around their vibrissal follicles than terrestrial mammals (Hyvärinen 1989, Marshall et al. 2006). Superficial and deep vibrissal nerves collect sensory information from the whisker follicles, and coalesce to form the infraorbital nerve, a maxillary division of the trigeminal nerve. Information from the whiskers enters the brain via the trigeminal nerve. In mammals that have organised whiskers, the whisker grid can appear in topographic structures through the brain, termed barrelettes in brainstem, barreloids in thalamus, and barrels in layer four of the somatosensory cortex (Fig. 2b). These structures have been detected in some rodents (mice, rat, hamster *Cricetus cricetus*; Woolsey et al. 1975), marsupials (wallaby *Macropus eugenii*; Woolsey et al. 1975, Waite et al. 2006), pinnipeds (California sea lion *Zalophus californianus*; Sawyer et al. 2016), and nocturnal primates (northern greater galago *Otolemur garnettii*; Sawyer et al. 2015), but are absent in the guinea pig *Cavia porcellus* and beaver *Castor fiber* (Woolsey et al. 1975), and many species have not yet been investigated. This one-to-one mapping of whisker signals ascending through the brain to somatosensory cortex has inspired many neuroscientists to use this system as a model of mammalian sensory processing, since signals can be traced from the whisker to the cortex. However, many other structures in the brain are also associated with whisker touch sensing, including the superior colliculus (Cohen & Castro-Alamancos 2010, Gharaei et al. 2018), cerebellum (Bower 1997, Bosman et al. 2010), striatum (Bosman et al. 2011), and zona incerta (Bosman et al. 2011, Evans et al. 2019). The interconnectivity of all these brain areas is complex and does not fit with the simple idea of ascending and descending sensorimotor pathways (Evans et al. 2019); this architecture needs to be better understood in order to understand the processing of whisker sensorimotor information fully.

Some mammals actively control their whiskers using specialist facial muscles, of which there are two types: intrinsic and extrinsic. Intrinsic whisker muscle architecture is largely conserved, from marsupials to primates (Grant et al. 2013a, Muchlinski et al. 2013). Even humans have vestigial whisker muscles in their upper lip (Tamatsu et al. 2007). The intrinsic muscles form a series of slings around each of the follicles in a row, such that all the whiskers in the same row move together (Dörfl 1982). In many rodents, such as mice and rats (Fig. 2c), a quick, continuous, to-and-fro cyclic movement, called whisking, is possible (Dörfl 1982, Haidarliu et al. 2010, Grant et al. 2013a, 2017, Haidarliu et al. 2021). It also manifests in other species (Vincent 1912, Grant et al. 2018, Muchlinski et al. 2020). Whisking is driven by a brainstem pattern generator (Kleinfeld et al. 2015) and occurs at 5 Hz in the opossum *Monodelphis domestica*, 8 Hz in rats, and up to 25 Hz in mice (Mitchinson et al. 2011). Higher proportions of type 2B muscle fibres are found in intrinsic muscles in high-frequency whisking mammals (mice) than in

lower-frequency whisking mammals (rats) and in non-whisking mammals (guinea pigs; Jin et al. 2004). Whisking is likely to have evolved to enable fast scanning of the sensory environment (Jin et al. 2004). Muchlinski et al (2020) present a comprehensive review of which mammals whisk; all whisking species tested are nocturnal and arboreal.

Some species-specific variation occurs in the intrinsic muscles; species with more disorganised whisker arrangements tend to have correspondingly more disorganised and thinner intrinsic muscles (Muchlinski et al. 2020). This disorganisation occurs in guinea pigs and nocturnal primates, which can move their whiskers using their intrinsic muscles but do not whisk. Pinnipeds have pronounced intrinsic muscles that enable underwater protractions (forward movements; Dehnhardt & Hanke 2018). However, these protractions are single, isolated movements, and not the continuous, cyclic, to-and-fro movements that are defined by whisking. Therefore, pinnipeds also do not whisk; indeed, whisking would likely require much effort underwater (Grant et al. 2013b, Milne et al. 2020).

As well as whisking and protractions, some mammals can make other, more complex movements with their whiskers, for example, changing whisker symmetry, speed, spread, and orientation. Such motions occur during object exploration and are termed contact-related behaviours (Mitchinson et al. 2007, Grant et al. 2009, Mitchinson et al. 2011). For example, when rats contact an object, they often reduce the spread of their whiskers, bunching them up to bring more whiskers into contact with the object. They also slow down whisker movements as they move across the surface, to increase contact times (Grant et al. 2009). Those behaviours are mainly controlled by extrinsic muscles, which sit external to the mystacial pad. Scientists have noted considerable variation in the extrinsic muscles of different species (Yohro 1977, Grant et al. 2013a), which may account for some of the species-specific behavioural differences observed in whisker use.

Collectively, the mystacial whiskers move around a volume of three-dimensional space surrounding the animal's face, referred to as the search space (Huet & Hartmann 2014). In general, the shape and orientation of that search space can be altered by the protraction (forward movement), elevation (upward movement), and rotation of the whiskers. The orientation of the search space may provide clues about the animal's attention (Mitchinson & Prescott 2013). To date, the only species for which the search space has been studied is the rat. When a rat's whiskers are relaxed, their tips lie on a near-spherical surface with the rat's eyes at the centre, suggesting that the vibrissal sensory system is registered with the rat's visual system (Huet & Hartmann 2014). Indeed, both tactile and auditory locations are mapped on to retinotopic visual maps within the superior colliculus in the mouse (Drager & Hubel 1976, Gharaei et al. 2018) and hamster *Mesocricetus auratus* (Tiao & Blakemore 1976). Perhaps having a physical, spatial overlap of these sensory systems enables efficient multisensory integration and localisation calculations (Grant & Arkley 2015). Given that whisker layout and search space are likely to be associated with whisker function (Grant & Arkley 2015), it would be interesting to study how those compare across species.

HOW DO WHISKERS DEVELOP?

Besides in laboratory rats and mice, researchers have only studied the development of whiskers in one other species – tammar wallabies *Macropus eugenii* (rats: Sullivan et al. 2003, Grant et al. 2012a, b; wallabies: Waite et al. 1991, 1998, 2006). Those studies report that whiskers emerge before pelage hair (Waite et al. 1991, Grant et al. 2012a). In rats and mice, whisker follicles appear in embryo and whiskers are present from birth (Landers & Zeigler 2006). By comparison, their eyes typically do not open until around postnatal day (P)13–14 (Landers & Zeigler 2006; Fig. 3, bottom) and the auditory system does not become functional until about P10 (Grant et al. 2012a). The precocial development of vibrissal touch suggests that it may constitute an important source of sensory information for newborn mammals. From as early as P3, stimulating rat whiskers causes heightened activity, and whiskers can guide nipple search and attachment and huddling movements in young rat pups (Sullivan et al. 2003, Grant et al. 2012b).

Most animals cannot move their whiskers at birth (Landers & Zeigler 2006). In rats, whisker movements start with small, unilateral retraction movements in the first postnatal week (Grant et al. 2012a). These can occur when the rats are sleeping, as small, asynchronous whisker twitches (Tiriac et al. 2012). Bilateral whisker movements are present from P7, with whisking emerging around P11 and becoming established by P13-14 (Grant et al. 2012a, Arakawa & Erzurumlu 2015). Those movements start as small twitches with low levels of amplitude and frequency and increase to adult levels by around P21 (Fig. 3, top). Contact-related modulation of whisking behaviour emerges gradually and becomes established by P17 (Grant et al. 2012a). It is unclear whether the delay of contact-related whisking behaviour is due to a lack of neural or muscular control in young animals, or whether they need sensory inputs and experience to develop these behaviours. Visual inputs can also influence the development of whisker shape; cats *Felis catus* and mice that are blinded from birth have larger whiskers and larger tactile cortical areas (Rauschecker et al. 1992).

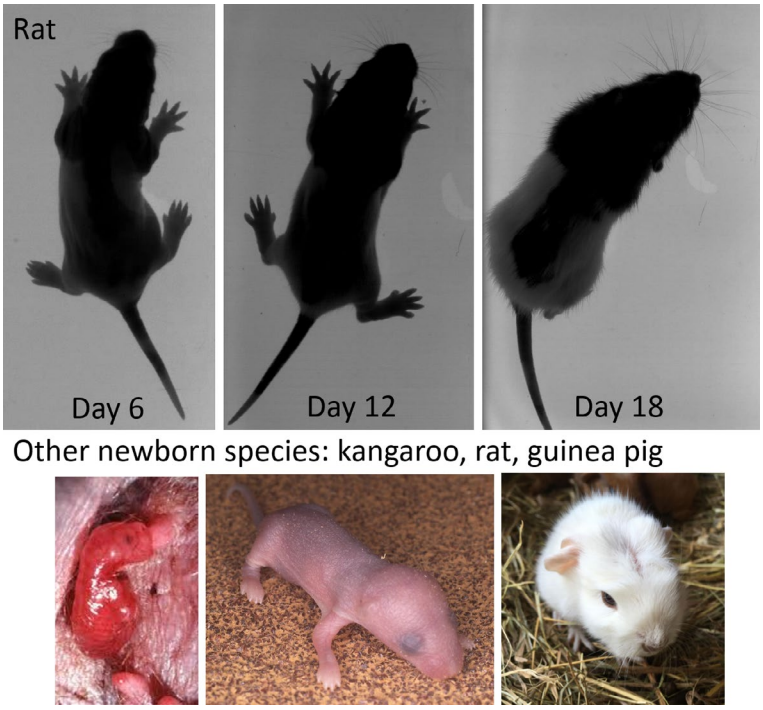

Fig. 3. Developmental schedules in mammals. Top row: whisker appearance during development in the brown rat *Rattus norvegicus* at postnatal days 6, 12, and 18. Bottom row: comparative developmental schedules in near-newborn kangaroo *Macropus* sp. (left), rat (centre), and guinea pig *Cavia porcellus* (right). Photographs: kangaroo: Geoff Shaw, Creative Commons; rat: Marco Bernardini, Flickr; guinea pig: Lindsey Cross, Lindsay's Animal School, East Sussex, UK.

Indeed, studies investigating how sensory experiences affect early brain development suggest that whisker sensations play an important role in shaping the connections, arrangement, and size of brain structures. The most well-studied area is the barrel cortex (in mice and rats). The spatial arrangement of whisker follicles on the snout provides a template for the formation of axonal and cellular patterns in the barrel cortex during a critical period in development from P1-5 (Erzurumlu & Gaspar 2012). During this period, whisker trimming, or removal of sensation from the vibrissal nerve, can have large effects on the patterning of neural elements within the barrel cortex (Lee et al. 2009, Erzurumlu & Gaspar 2012), as well as on thalamocortical projections and other areas of the cortex (Erzurumlu & Gaspar 2012). This can, in turn, have profound behavioural deficits later in life (Lee et al. 2009, Simanaviciute et al. 2020). For example, trimming rat whiskers P0-3 can affect adolescent rat locomotion, exploratory, and social behaviours in the long term (Lee et al. 2009). Therefore, the first week of life is a critical period for rats and mice, and experiencing natural whisker sensation is key to shaping their brain and behaviour during this time.

Research indicates that whisker emergence and movement vary according to a species' developmental schedule. For example, the absence of whiskers in tammar wallabies might be expected, since marsupials are immature at birth (Waite et al. 1991), whereas rats, which are more mature at birth, are born with intact (but immobile) whiskers (Grant et al. 2012a; Fig. 3). Their whisker movements subsequently develop alongside their locomotion abilities, until the third postnatal week. Guinea pigs, even more mature at birth, are endowed with a full range of locomotor abilities at birth (Fig. 3; Oakley & Plotkin 1975). Consequently, although not yet tested, we predict that they are born with more adult-like whiskers and may be capable of the simple, unilateral whisker movements that adult guinea pigs make (Fig. 3, bottom). However, to draw general conclusions about whisker development requires data from a more diverse group of mammals.

HOW DID WHISKERS EVOLVE?

Although whiskers do not appear in fossil records, comparative studies of extant species combined with developmental studies offer ways to infer ancestral relationships and understand the evolution of whiskers (Müller 2007). It is not yet known whether whiskers evolved independently of pelage hair, nor whether whiskers appeared before or after pelage hair. Various hypotheses have been

proposed. Some researchers point to the morphological differences between whiskers and hair, which they see as evidence for independent evolution (Pocock 1914, Ahl 1986). In agreement with this, Chernova (2006) suggested that whiskers could have evolved directly from mechanoreceptors and, if so, were probably always tactile sensors. Alternatively, whiskers may have evolved from pelage hair – from the epidermis or prototrichs. The first hair-like structures on the body, or tylotrichs, were probably distributed across the body surface (Maderson 1972) and may have arisen from modified mechanosensory areas located at scale hinges in synapsids (Maderson 1972, Alibardi 2004). Certainly, pelage hair and whisker α-keratin genes are both closely associated with modified keratin-rich structures, such as claws (Eckhart & Ehrlich 2018) and penile spines (Reno et al. 2013). Maderson (1972) hypothesised that these first hair-like structures were probably tactile, rather than thermoregulatory. However, it is also speculated that these hair-like structures may have been associated with sebaceous glands (Chernova 2006, Dhouailly 2009).

Whiskers, and their neural and muscular architectures, are present and conserved in the majority of extant mammal species – from marsupials to primates (Grant et al. 2013a, Muchlinski et al. 2013, 2020). However, they are lacking in monotremes. The conservation of whiskers, muscles, and their neural structures in therian mammals has prompted some researchers to suggest that a common ancestor of placental and marsupial mammals probably had whiskers (Waite et al. 1998, Grant et al. 2013a, Benoit et al. 2016, Fig. 4) that may have also been actively moved (Mitchinson et al. 2011, Grant et al. 2013a). The last common ancestor of placental and marsupial mammals has been dated to be at least from the Late Jurassic with the fossil eutherian *Juramaia* (Luo et al. 2011), or even the Early Jurassic (dos Reis et al. 2014). However, Benoit et al. (2016) have proposed that facial whiskers were present and functional in therapsids even earlier – 240–246 million years ago (Benoit et al. 2016). If this is the case, then it is likely that whiskers guided early mammals and their ancestors to orientate themselves nocturnally within complex environments (such as in trees), which is what we observe in many mammals today.

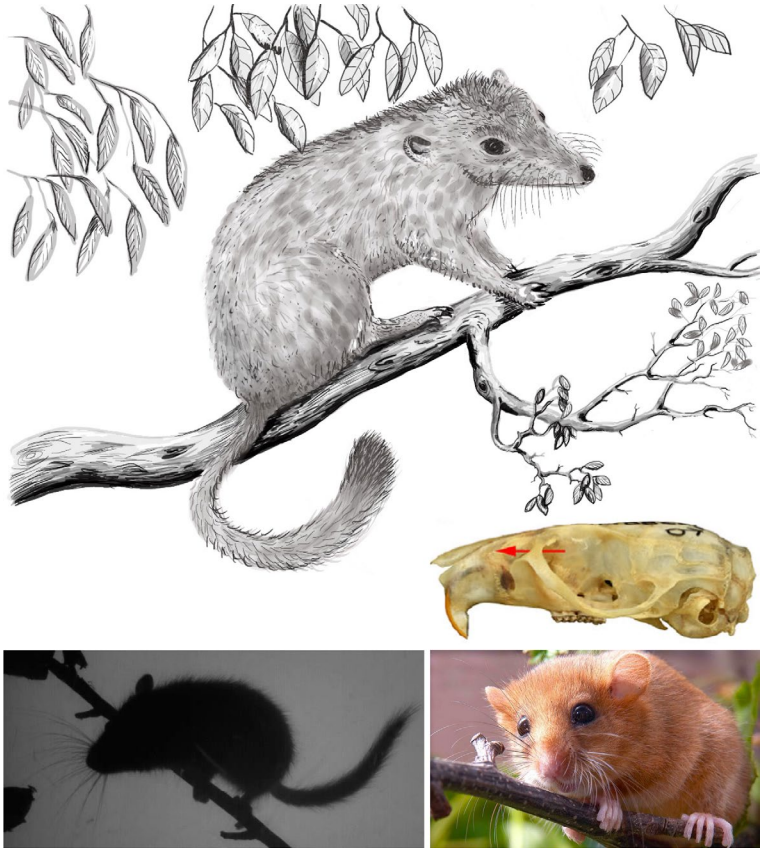

Fig. 4. Top: Example sketch of an extinct, nocturnal climbing mammal (Geoff Goss, London South Bank University, UK); bottom: extant, nocturnal, climbing mammals (e.g. hazel dormice *Muscardinus avellanarius,* shown here) have long, slender whiskers and a large infraorbital foramen (arrow on rodent skull). Dormouse photograph: Terry Longley, the Wildwood Trust, Kent, UK.

When researching the evolution of whiskers, it is instructive to reflect on the manifestation of whiskers and the ecology of extant mammals. For example, fossil evidence suggests that burrowing was probably important for synapsids and therapsids – the early ancestors of mammals (Damiani et al. 2003). Burrowing remains a prevalent trait in extant mammals, and many burrowing species, such as the star-nosed mole *Condylura cristata* (Catania 2020) and the naked mole rat *Heterocephalus glaber* (Crish et al. 2003), make use of mechanosensation to feel vibrations underground. Numerous locomotor modes and substrate preferences are inferred in stem and crown group mammals from the Middle Jurassic onwards (Luo 2007, Chen & Wilson 2015); however, climbing adaptations are particularly well represented (Goswami et al. 2011, Chen & Wilson 2015, Meng et al. 2015). Since many extant whisker specialists are nocturnal, arboreal mammals, climbing may have played a role in whisker specialisation in the first mammals. We propose that whiskers provided tactile guidance while climbing in the dark, in these early species. Sensory integration between vision, olfaction, and whisker touch is an important driver of brain evolution, and a likely cause of the enlarged cortex in mammals (Rowe et al. 2011).

The lack of whiskers and associated musculature in the fossil record is a major handicap for studying the evolution of whiskers. However, bony structures associated with whisker processing and movements could provide surrogate measures. One such structure is the infraorbital foramen (IOF), a small hole in the skull through which the infraorbital nerve passes (Muchlinski 2010; Fig. 4). The size of the IOF is correlated with the size of the infraorbital nerve and is a good measure of maxillary somatosensory acuity (Muchlinski 2010). The IOF is also larger in species that whisk (Muchlinski et al. 2020), suggesting that whisking mammals probably have more sensitive whiskers than non-whisking mammals. Examination of IOF areas in fossil specimens and ancestral character state reconstructions indicate that it is unlikely that early mammals engaged in whisking (Muchlinski et al. 2020). However, that does not rule out other, more simple protraction movements, as observed in pinnipeds and felids. Indeed, reconstruction of the skull of the non-mammaliaform therapsid, Prozostrodontia, showed it to have an infraorbital canal that was more similar to that of mammals than that of basal therapsids. The presence of a true infraorbital canal in Prozostrodontia suggests that facial whiskers were present and functional in this group (Benoit et al. 2016), although we are not able to infer much about the whisker movements (Muchlinski et al. 2020). Predictions relating to the whisker movements of early mammals may be viable by means of ancestral state reconstruction, using quantitative whisker movement data from many, diverse extant mammalian species. That would require collecting natural and comparable whisker movement data across a range of species, which presents a challenge.

WHAT ARE WHISKERS FOR?

While it is clear that whiskers engage in touch sensing, how they are employed naturally in an animal's life is often unknown. The observation that nocturnal, arboreal, and aquatic mammals tend to have relatively long, organised whiskers suggests that whiskers play a key role in helping a mammal to orient itself in dark, complex environments. This is consistent with research that shows whiskers guiding locomotion in small, quadrupedal mammals, including shrews *Suncus etruscus*, *Sorex minutus*, *Neomys fodiens*, rats *Rattus* spp., mice *Apodemus sylvaticus*, *Apodemus flavicollis*, *Micromys minutus*, dormice *Muscardinus avellanarius*, guinea pigs *Cavia porcellus,* and voles *Myodes glareolus*, *Arvicola amphibious* (Grant et al. 2018). For example, on a flat or inclined floor, whiskers are used to guide the placement of forepaws during forward locomotion (Arkley et al. 2014, Grant et al. 2018). Research on hazel dormice *Muscardinus avellanarius* (Arkley et al. 2017; Fig. 4) and rats (Vincent 1912, Gustafson & Felbain-Keramidas 1977, Jenkinson & Glickstein 2000) shows that whiskers assist in the guidance of foot placement during tasks such as climbing, edge-following, and gap-crossing.

The whiskers of many aquatic mammals, such as pinnipeds and sirenians, plus those of certain semi-aquatic mammals (Eurasian otter *Lutra lutra* and European mink *Mustela lutreola*) tend to be notably thicker and stiffer than those of terrestrial mammals (Ginter Summarell et al. 2015, Dougill et al. 2020). Stiffness measurements have only been undertaken on dry samples so far (Ginter Summarell et al. 2015), and it is likely that whiskers will be less stiff and behave quite differently in the water (Leveque 2005). Nevertheless, pinnipeds have remarkably distinctive whiskers; those of seals (Phocidae) are flattened and have an undulating profile (like a sine wave), while those of sea lions (Otariidae) have elliptical cross-sections and are smooth (Ginter et al. 2009, 2012). These traits reflect evolutionary adaptations to aquatic environments. For example, studies suggest that that oval, undulating whisker profiles are more efficient for sensing underwater, since the undulations cause vortex shedding around the whiskers (Ginter et al. 2009, Hanke et al. 2010, Ginter et al. 2012, Dehnhardt & Hanke 2018). As well as for touch sensing, seals and sea lions use their whiskers for hydrodynamic sensing (Dehnhardt et al. 2001, Gläser et al. 2011, Dehnhardt et al. 2014) and are capable of following the wakes of fish as they swim through the water. Pinnipeds that hunt moving prey, such as fish, are thought to have

more moveable whiskers than those that do not, such as walruses (Milne et al. 2020). Indeed, Pocock (1914) observed that aquatic and semi-aquatic hunters, such as water opossum *Chironectes minimus*, giant otter shrew *Potamogale velox*, and Eurasian otter have long, thick whiskers, whereas semi-aquatic herbivores such as the Sirenia, Hippopotamidae, and capybara *Hydrochoerus* spp. have much smaller whiskers, although they tend to be more numerous. Therefore, as well as guiding locomotion, whiskers are also important for foraging and hunting, especially in mammals that hunt moving prey items in the dark. However, there are departures from this. Some mammals have reduced whisker size and functionality, and, rather, rely on other specialised senses to find prey in the dark, for example echolocation in cetaceans (Yablokov et al. 1972) and bats (Wetterer et al. 2000). Cetaceans are a particularly interesting group, since they can have very short whiskers (mysticetes and river dolphins *Plantanista indi*; Fig. 1), or even absent whiskers (beluga whales *Delphinapterus leucas* and narwhals *Monodon Monoceros;* Yablokov et al. 1972). Some delphinids (Guiana dolphin *Sotalia guianensis*) are even born with whiskers, but shed them during development, and their intact follicles are used for electrosensing instead (Czech-Damal et al. 2012). We know very little about why whiskers may be prominent in some species and lost in others. However, whiskers are a useful proximal (close-up) sense for prey detection in many mammalian species who hunt in dark environments.

Indeed, whiskers have been observed to guide head-turning and attacks towards prey items, for example in rats (Grant et al. 2012b, Mitchinson & Prescott 2013), shrews (Anjum et al. 2006), and pinnipeds (Milne & Grant 2014, Milne et al. 2020). The Etruscan shrew *Suncus etruscus* uses its whiskers to locate spikes on the back legs of a cricket. It then targets its attacks there, removing the cricket's legs to prevent it from escaping (Anjum et al. 2006). Whiskers can extract a variety of physical properties from a prey item or object, including texture, size, and shape. Examples of this have been documented for rodents (Carvell & Simons 1995), pinnipeds (Dehnhardt & Dücker 1996, Grant et al. 2013b), mustelids (otters; Strobel et al. 2018), and sirenians (Reep et al. 2001).

Whiskers also play a role in social interactions (Wolfe et al. 2011) and are especially important in allowing young mammals to maintain contact with their mother and conspecifics (Sullivan et al. 2003, Grant et al. 2012b). Rats have been observed to make contact with each other's whiskers when they first encounter one another. For example, when rats 'box', a form of upright aggressive behaviour, the defending rat attempts to keep whisker–whisker contact, to enable the detection of a lunge or attack from its opponent (Ahl 1986, Barnett 2007). Boxing does not usually occur in rats that have had their whiskers removed. Some rats and mice even engage in barbering (Strozik & Festing 1981), whereby they remove another's whiskers, usually those of an animal lower in the dominance hierarchy, presumably to prevent fighting. Mother cats sometimes also trim their offspring's whiskers, perhaps to establish a dominance hierarchy or to keep the kitten close to the nest (Ehrenlechner & Unshelm 1997).

Vibrissal removal in rodents has been associated with an emotional component and can decrease motivation in the laboratory rat (Vincent 1912, Ahl 1986), as well as increase stress. Indeed, whisker trimming and removal reduces the social and locomotor functioning of an individual (Vincent 1912, Ehrenlechner & Unshelm 1997), and also negatively impacts brain development. Given that whisker removal negatively affects social and locomotor behaviours, tactile enrichment may well have positive effects on mammals, especially captive ones. For example, stroking the whiskers and adding tactile cage enrichment in laboratory rodents has been shown to increase neural connections, plasticity, and amplitude of responses in the somatosensory cortex (Welker et al. 1992, Landers et al. 2011) and also enhances exploratory behaviours (Frostig 2006, Landers et al. 2011).

APPLICATIONS OF COMPARATIVE WHISKER STUDIES

Animal welfare

Given the importance of whiskers for exploration, foraging, and social interactions, it follows that the welfare of a captive mammal will be enhanced if it has a diverse range of objects and surfaces to manipulate tactually and interact with (similar to the way scents are used for sensory enrichment), especially from a young age. Also, facilitating tasks that encourage naturalistic whisker movements, such as during feeding, training, or play, should help replicate natural whisker movements and sensations (Milne & Grant 2014, Milne et al. 2020), which has implications for muscular, sensory, and neural enrichment. That would be especially important for animals that use their whiskers actively for foraging, such as insectivorous shrews and rodents, as well as piscivores (otters, pinnipeds). Similarly, including a range of textures and climbing frames in enclosures for mammals that use their whiskers for orientation, especially small, nocturnal mammals, would be beneficial for them.

It is not just mammals in captivity that can benefit from tactile environmental enrichment. Landscapes of homogenous textures containing isolated populations and individuals will also reduce whisker stimulation. Captive hazel dormice use their whiskers to guide locomotion and

gap-crossing in a climbing arena (Fig. 4). However, when gaps were introduced to walkways that were larger than the animals' whisker spans (>15 cm), the dormice spent longer on the floor of the enclosure, more time travelling, and less time feeding (Arkley et al. 2017). Arkley et al. (2017) suggest that gaps in typical dormice habitats, such as in woodlands and hedgerows, might have a similar effect on wild dormouse behaviour. That supports the notion that the establishment of wildlife corridors, which include densely constructed hedgerows, will improve the welfare of small, arboreal whisker specialists, such as rodents.

Conservation physiology and individual identification

Whisker research may also have applications for mammalian conservation and ecology. The isotope ratios of inert keratinous tissues reflect an animal's foraging and movement patterns over the period of tissue synthesis (Robertson et al. 2013, Kernaléguen et al. 2016, McHuron et al. 2019). Since whiskers grow continuously, they can serve as a long-term storage of useful biochemical information, which is especially useful for isotope analysis (Robertson et al. 2013), as well as tracking reproductive and stress-related hormones (Keogh et al. 2021). Whisker isotope analysis has been successfully investigated in European badgers *Meles meles* (Robertson et al. 2013), Tasmanian devils *Sarcophilus harrisii* (Bell et al. 2020), brown fur seals *Arctocephalus pusillus* (Kernaléguen et al. 2016), northern elephant seals *Mirounga angustirostris* (McHuron et al. 2019), American mink *Neovison vison* (Bodey et al. 2010), and sea otters *Enhydra lutris* (Newsome et al. 2009). However, to interpret the results of such studies fully, researchers require precise knowledge of vibrissal growth rates, shedding, and moult. Of the few whisker life-cycle studies that have been carried out, most find linear growth rates, e.g. in mice, rats, and pinnipeds, such as Steller sea lions *Eumetopias jubatus* (Ibrahim & Wright 1975, Hirons et al. 2001, Greaves et al. 2004). The most in-depth whisker growth studies, performed in laboratory rodents (Ibrahim & Wright 1975), found that whisker growth was linear and occurred at 1 mm a day in the mouse and 1.5 mm a day in the rat (see the growing rat whisker lengths in Fig. 3, top). However, research into certain phocid species, including harbour seals *Phoca vitulina* and grey seals *Halichoerus grypus*, shows that whisker growth can be intermittent (Hirons et al. 2001, Greaves et al. 2004). This may present difficulties in identifying when isotopes become incorporated into the tissue (Greaves et al. 2004), which researchers seeking to extrapolate diet and movement data from whiskers will need to address.

Spurr (2002) demonstrated that whiskers could be used to identify individual stoats *Mustela erminea* that have eaten bait tagged with Rhodamine B, a dye that causes hair to have an orange-red fluorescent band. Assuming a linear growth rate and observing that a stoat's whisker remains intact for about five months, the identity of individuals could be determined from the position of the fluorescent band along the whisker, corresponding to when that individual ate the tagged bait (Spurr 2002). Such a method may be used to estimate the proportion of the stoat population that would eat bait to judge the suitability of using toxic bait for population control.

Pennycuick and Rudnai (1970) reported that the positions of whiskers on a mammal's muzzle differ from one individual to another (Fig. 5). They proposed that this could be used to identify individuals. That idea has since been taken up with respect to lions *Panthera leo*, Australian sea lions *Neophoca cinerea,* and polar bears *Ursus maritimus* (Packer & Pusey 1993, Anderson et al. 2016, Osterrieder et al. 2017), now using software to analyse whisker positions automatically from photographs. Whisker function and use remain undescribed in both lions and polar bears, perhaps due to the challenges of clearly observing and measuring their whiskers in zoo enclosures or natural habitats. Furthermore, the factors that affect variations in whisker position have yet to be explored, although diet, health, age, genetics, and other environmental factors may all play a role. While the technique has only been trialled on a few species so far, it offers a potentially powerful, non-invasive tool in individual recognition studies. It is now important to investigate the determinants of individual whisker arrangements in a range of species, and to track whisker arrangements through the life span of individuals, to ascertain the reliability and robustness of using whiskers as an identification tool.

FUTURE RECOMMENDATIONS

The lack of systematic, comparative whisker biology studies makes it difficult to address broad-scale questions in evolution and function. A large-scale comparative dataset recording whisker length, number, IOF area, and the presence of whisking for 204 mammalian species (Muchlinski 2010, Muchlinski et al. 2020) does not capture all the variations in whisker movement and arrangements observed across mammals. Certainly, long, organised, mobile whiskers with highly sensitive follicles are found in species that hunt moving prey in dark, complex environments, such as in tree canopies and under water. Radical departures from those forms are also observed, such as the undulating whiskers of Phocidae and the complete loss of whiskers in some cetaceans. This begs the question, what kinds of changes in whisker form can emerge with respect to whisker

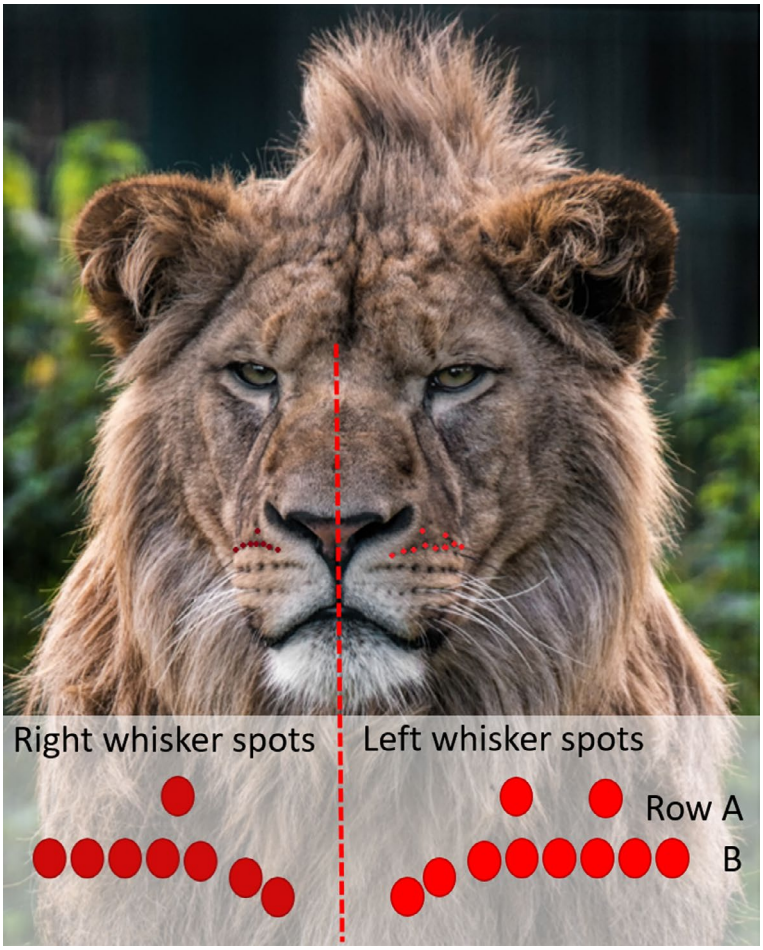

Fig. 5. Identification of lion *Panthera leo* whisker follicle patterns, based on descriptions from Pennycuick and Rudnai (1970). The two dorsal-most whisker rows are used to identify whisker follicle positions on each side. Photograph: Shaun Wilson, Blackpool Zoo, Blackpool, UK.

function? If we are to start seeking answers to such a question, then we require systematic, comparative behavioural and morphological studies that embrace a far wider range of species.

With the development of non-invasive camera technologies, lighting and image tracking algorithms (Gillespie et al. 2019, Simanaviciute et al. 2020), we should now be able to describe whisker movements during natural behaviours, including locomotion, hunting, and social interactions. This will also help us understand the impact of human-designed environments on mammals in laboratories, in zoos, and in places where human activity has disturbed natural habitats. Moreover, studying whisker use of mammals in their natural habitats will help us to understand mammalian sensing and behaviour, more generally.

Anatomical studies of whisker arrangement, growth, and shape provide indicators for interspecies comparative studies. Identifying which factors affect whisker arrangement and growth will also help us to assess their use in biochemical analysis studies, and their application as robust individual identification markers.

CONCLUSIONS

In concluding this review, we hope to have highlighted that whisker research has advanced a long way since the early 20th Century pioneers: Vincent, Pocock, and Beddard. The bulk of whisker research since has focused on rodents, marsupials, and pinnipeds. In all species investigated, whiskers are slender, curved, tapered, keratinised hairs that transmit vibrotactile information from the whisker hair, through the follicle, to specialist structures in the brain. In many species, whiskers appear in embryo and prior to the development of other senses. They probably play an important role in many young mammals, including locating the nipple for feeding and staying in close contact with the mother and conspecifics. Whiskers are moved using a network of intrinsic

muscles that are present in many mammalian species, including marsupials and primates. The conservation of whisker form and a common muscle architecture in mammals suggests that early mammals had whiskers. Indeed, whiskers may have even been functional in therapsids. However, we show here that there are also marked differences between species with respect to whisker arrangement, numbers, length, musculature, developmental schedules, and growth cycles. Certainly, some species are equipped with especially long and sensitive whiskers, and these tend to be nocturnal, arboreal species, and aquatic species, which hunt moving prey.

This review highlights that if we wish to extend our understanding of how whisker form relates to function, then the research must extend to encompass a wider range of species. Developments in new technology and analysis techniques can facilitate that extension.

We propose that comparative biology offers opportunities to explore associations with whisker function and evolution across mammalian species. Such research should also inform us of habitat features that are important for different species, which also has implications for animal welfare and conservation.

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